DESCRIPTIVE ETHOLOGY AND ACTIVITY PATTERNS OF BLACK-FOOTED FERRETS

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ABSTRACT. —Aspects of the aboveground ethology and activity patterns of the black-footed ferret (Mustela nigripes) are described for a population in northwestern Wyoming as a first step in building a descriptive ethogram and quantification of activity patterns. We observed at least 237 individual ferrets for 208 hr on 441 occasions from 2 December 1981 through 25 September 1984. Maintenance behaviors (locomotion, alert, grooming and sunning, defecation and urination, digging, and predation) and social behavior (reproduction, ontogeny, maternal, play, agonistic) are described as well as some ferret-human interactions. Ferret vocalizations are subjectively described. We located ferrets during most months, including winter, but found that they were easiest to locate in summer. Ferrets were active at -38 C, in snow, in rain, and in winds to 50 kph.

The black-footed ferret (BFF) is one of the least well known of all the endangered mammals in the United States despite 11 years (1964-1974) of intensive and extensive research in South Dakota (Erickson 1973, Hillman and Linder 1973). Data are lacking on many aspects of BFF behavior and activity patterns. It is essential that the general behavior patterns of any animal first be qualitatively described in an "ethogram" to provide the basis for more specific, quantitative behavioral studies (Scott 1956, Klopfer and Hailman 1967, Lehner 1979). This paper provides an initial description toward a BFF ethogram and gives results of nocturnal observations of surface activity for the Meeteetse, Wyoming, BFFs. Behavioral descriptions are "functional" (Candland 1974) and definitions are operational (Sustare 1975).

METHODS

Behavioral descriptions are based on 208 hr of direct observation of at least 237 individual BFFs on 441 occasions between 2 December 1981 and 25 September 1984. We observed maternal, play, and predatory behavior at 10 m or less, sometimes for over 1 hr per observation. Daytime observations were generally made with the unaided eye, but a spotting scope and binoculars were sometimes used. Nighttime observations were made with the aid of hand-held or truck roof-mounted spot-

lights following methods outlined by Clark et al. (Handbook of methods, 1984). The time and duration of each observation, description of behavior, and weather conditions were recorded, and photographs were taken when possible. Because BFFs are nocturnal, secretive, solitary, and active above ground briefly and irregularly and because they inhabit an environment of grass and shrubs, it is very difficult to observe and collect a complete picture of their ethology. Some BFF behavior (e.g., locomotor, predatory) was in part inferred from 243 BFF snow-tracking records collected over three winters 1981-1984 (Richardson et al. 1985 and unpublished data). Our behavioral descriptions were facilitated by earlier behavioral observations (by TWC) of steppe ferrets (M. eversmanni, 32 hr) and European ferrets (M. putorius, 123 hr), as well as by ethological studies on other species. Where appropriate, we compare our observations with the literature on BFFs and other mustelids.

RESULTS

We describe individual maintenance, intraspecific social, and interspecific behavior patterns (the three major behavioral categories often recognized; e.g., Balph and Stokes 1963), as well as BFF vocalizations. Photographs of some of these behaviors and BFF signs are in the Appendix.

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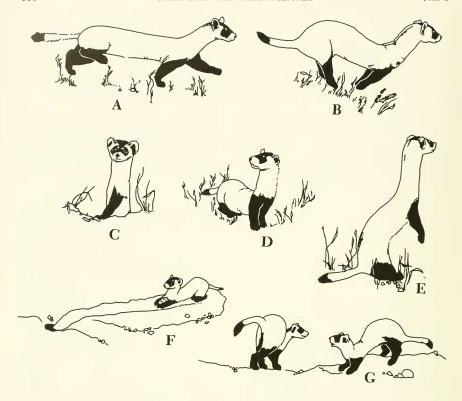


Fig. 1. Some black-footed ferret motor patterns and body postures: A, Walking. B, Bounding. C, In-burrow alert posture. D, All-fours alert posture. E, Upright alert posture. F, Digging, G, Play.

Maintenance Behavior

Maintenance behavior is performed by an animal in the normal course of its daily activities and is critical to its survival.

Locomotion.—BFFs either walked or bounded (Fig. 1). Walking is a forward progression in the typical quadruped manner—a cross-wise stepping movement. Forward movement of the left front leg was followed by the right hind leg, then the right front leg was followed by the left hind leg. The head was usually held above the torso but was occasionally lowered as if to sniff the ground. The tail was usually held off the ground, at a variable downward angle from the torso. BFFs walked about 2% of the distance traveled per winter night, typically near prairie dog burrow entrances.

Bounding is a leaping run or gallop in which both hind feet and then both front feet are alternately set before one another, with the hind feet set fairly accurately in the twin tracks of the front feet. Travel between prairie dog (Cynomys leucurus) holes and long distance movements were in this gait. BFFs often traveled in vegetation-free areas such as cattle and game trails, roads, snow-filled gullies, and windblown hill crests. Relatively straight line movements of 75 m were common.

Hillman (1968), Henderson et al. (1969), and Fortenbery (1972) described BFF movements between prairie dog burrow openings as "running." They did not describe walking or bounding locomotion; however, photographs of BFF tracks in snow in Fortenbery (1972) were the bounding type.

Alert behavior.—Alertness composed a high percentage of BFF behavior and was the only activity that frequently interrupted all others. Alertness was characterized by: (1) inburrow alert posture ("periscope"), in which only a BFF's head, part of the head, or upper torso was visible; (2) down alert posture, aboveground alertness in which all four feet were on the ground; and (3) upright alert posture, in which the BFF stood on its hind feet, balancing with its tail and hind legs, with its forelegs off the ground (Fig. 1). An immobile body was the common element of the different alert postures.

The in-burrow alert posture or periscope was by far the most common alert posture. The down alert often occurred between bursts of locomotion, especially if the BFF was hunting in tall vegetation with the prairie dogs active nearby. The upright alert posture was less frequently observed under similar circumstance and was of very short duration.

Alert postures have not been described for BFFs. However, Fortenbery (1972) noted that BFFs may look out of prairie dog burrows, with only their heads showing (our inburrow alert). The limited descriptions and photos in Henderson et al. (1969:7,11) and Fortenbery (1972) suggest that the BFFs in Wyoming and South Dakota have similar repertoires of alert postures.

Grooming and Sunning.—BFFs scratch, mouth, and bite at their fur. These activities are functionally related to dressing the pelage, cleaning the body surface, and removing parasites (Eisenberg 1968). Scratching (n=8) consisted of perpendicular movements of one hind leg directed at various points on the body. Mouthing movements (n=4) are complex and variable and consisted of "biting" fur on the tail, legs, and ventral and lateral areas of the torso. Grooming of fur was evidenced by BFF hairs found in BFF scats. Washing or licking were not seen. Ticks were relatively common behind the ears, on the upper neck, and under the chin of adult BFFs. BFFs bit at flies that flew near their faces. We also observed BFFs yawn while sunning, where the head is thrown back, mouth opened full gap, and eyes closed.

Henderson et al. (1969) noted that an adult female BFF scratched a scab on her head with her hind paw and that young and adult BFFs seemed bothered by external parasites (ticks, fleas, and flies) and frequently scratched themselves. However, motor patterns were not described. Henderson (personal communication 1983) observed BFFs in South Dakota yawn.

Sunning consisted of lying sternally stationary on prairie dog mounds in sunlight. We observed this three times in midsummer between 0800 and 1100 hrs Henderson et al. (1969) noted that adult BFFs often basked in the warm, midmorning sun for several hours on prairie dog mounds during the young care period (July-August), fall, and spring. Progulske (in Henderson et al. 1969:7) reported sunning behavior in a captive adult male BFF. Henderson (personal communication 1983) observed BFFs basking in the sun in the snow.

Defecation and urination.—About 75 scats of possible BFF origin and an additional 15 of known BFF origin were found from December 1981 to January 1984 and are shown in Clark et al. (Handbook of methods, 1984). Of scats of probable BFF origin, two were found on top of each of two badger (Taxidea taxus) scats, several on BFF diggings, five beside a frozen BFF corpse in February 1982, and nearly all others near prairie dog burrow openings. Urinations (n=114) along snow-track routes were generally located near burrow entrances but did occur in midroute (Richardson et al. unpublished data).

Henderson et al. (1969) noted that scats and urinations were deposited separately, usually near a burrow mound, but the salient feature of BFF scats is that they are seldom found (Hillman 1968, Henderson et al. 1969, Fortenbery 1972). Hillman (1968) assumed and Henderson et al. (1969) suspected that BFFs defecate underground. Droppings of a captive adult male BFF were deposited in one corner of the pen during summer and in the burrow box during winter (Progulske 1969). Sheets and Linder (1969) recovered BFF scats from prairie dog burrows they excavated by machine.

Digging behavior.—BFFs excavate subsoil from prairie dog burrows and deposit it in a distinctive manner (Hillman 1968, Henderson et al. 1969, Hillman and Linder 1973, Hillman and Clark 1980, Clark et al. Seasonality of black-footed ferret diggings, 1984) (Appendix). We watched BFFs dig on nine

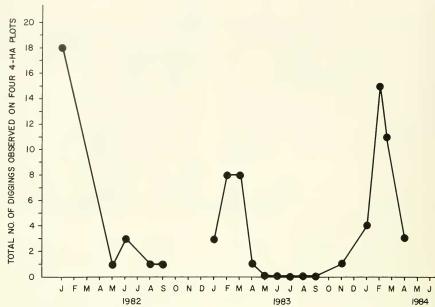


Fig. 2. Total number of ferret diggings observed on four 4-ha (16 ha) plots within the Meeteetse black-footed ferret habitat.

occasions, including the formation of two "diggings" or "trenches," as these structures were usually labeled by earlier observers. We prefer the word "diggings," since the subsoil is piled on the ground outside a prairie dog burrow and not dug into the soil surface as implied by the term "trench." When digging in a prairie dog burrow, BFFs back out of the tunnel with loosened subsoil held against their chests by their front feet. They drag the material further from the entrance with each trip (Fig. 1). The subsoil is sometimes pushed under the BFF's body, which may then arch forward, with the hind feet kicking soil further backward (pictured in Henderson et al. 1969: 15). BFFs also dig furrows in snow several centimeters deep, but we have not observed how these are made.

We observed results of BFF digging mostly during winter, when white-tailed prairie dogs were hibernating, but evidence of BFF digging was noted during all other seasons (Clark et al. Seasonality of black-footed ferret diggings, 1984; Clark et al. Handbook of methods, 1984) (Appendix). The frequency of occurrence and density of BFF diggings were

seasonally marked on four, four-haplots (Fig. 2). BFF diggings may be related to food acquisition. Seasonal peaks in diggings that could be identified as BFF occurred Ianuary-March and dropped to near zero by May each year. Both peaked in January, based on samples taken from January through December 1982, as described by Clark et al. Seasonality of black-footed ferret diggings, 1984; Clark et al. Handbook of methods, 1984) at about 4% and 2.5/ha, respectively, then dropped to near zero in April and remained very low until October, when they began to increase. South Dakota researchers agree that winter is the best time to look for BFF diggings: Hillman (1968) reported seeing BFF diggings in snow. Fortenbery (1972) noted that BFF diggings made during winter may persist for a long time. Henderson et al. (1969) observed more diggings in winter and in areas with small prairie dog populations. The excavated material may have been previously excavated by prairie dogs and subsequently brought to the surface by BFFs. The function of digging snow trenches is unknown. Hillman (1968) and Henderson et al. (1969) concluded that no

other mustelid that visits prairie dog colonies digs or leaves subsoil deposited in a manner like BFFs, but other mustelids and prairie dogs do excavate subsoil. An adult female BFF on 8 August 1983 moved eight stones (seven about 2.5 cm in diameter and one about 12 cm long, 5 cm wide, and 2 cm thick) from the burrow mound into her burrow over 22 mins. Each stone was individually moved, in the cases of the seven small stones, with the mouth, and the single large stone was dragged with the forelegs. The function of this activity is unknown.

Predatory behavior. - BFFs presumably obtain prev mostly at night below ground inside prairie dog burrows. Our snow tracking indicated that, in addition to taking prairie dogs, BFFs also take small rodents (Peromyscus maniculatus), and lagomorphs. During daylight in summer we saw BFFs kill prairie dogs and drag them to other holes on five occasions. During summer, one BFF leaped 0.7 m onto an adult prairie dog emerging from a hole and bit the back of the prairie dog's head. The BFF and prairie dog fell down inside the hole during the struggle. Two minutes later, the BFF emerged holding a prairie dog by the throat. The kill was dragged 10 m to a hole containing at least part of the female BFF's litter. Nine prairie dogs were on the surface within 40 m just prior to the kill. Another BFF ran 10 m to, and descended down, a hole that a prairie dog had just descended. The upper body of the prairie dog emerged from the hole but apparently was dragged back down by the BFF biting its posterior. Two minutes later the BFF emerged dragging a dead prairie dog by its throat. On two occasions, a BFF ran up to a prairie dog burrow opening, stopped with its body head first halfway down the hole, and waited motionless about 4 mins. At this time, the BFF dove into the tunnel, and prolonged high-pitched prairie dog "screams" and BFF "growls" emanated from the tunnel. On both occasions, the BFF emerged with a dead prairie dog within 5 mins. In all the above cases of predation, the prairie dog prey had a bloody throat and no other observable wounds.

On one occasion, a BFF bounded through the tall grass and shrubs and flushed out a ground squirrel (*Spermophilus armatus*). Within three additional bounds the BFF leaped on the back of the fleeing squirrel and seized it with a bite to the base of the skull. The BFF then descended a nearby ground squirrel burrow carrying the dead squirrel. Another BFF dragged two juvenile prairie dogs, one at a time, near us and dropped one. The killing bite appeared to be between the shoulder blades. Another time, a BFF ran toward a prairie dog 5 m away above ground but did not enter the hole the prairie dog retreated down.

BFFs are active in winter, exploring various burrows along their movements. Once a BFF enters a burrow, presumably it locates and captures prey by sound and smell. It sometimes takes prev above ground away from burrows. BFFs may remain below ground for several days in the same hole (Richardson et al., unpublished data). Prev were apparently often consumed below ground in burrows where kills were made. BFFs dragged prairie dog carcasses to another hole. One such kill found along a BFF drag exhibited punctures and hemorrhaging in the neck area behind the head (Appendix). In winter BFFs do not use any one burrow as a long-term nest burrow and may use some burrows as "cache" burrows (Richardson et al., unpublished data).

Our observations of BFF "hunting" behavior and those described by Hillman (1968), Henderson et al. (1969), Hillman and Linder (1973), and Fortenbery (1972) indicate that the BFF is a "searcher" predator (Alcock 1975). Our observations and those by Hillman (1968), Henderson et al. (1969), and Progulske (1969) in South Dakota are similar and suggest that killing behavior is stereotyped. BFFs kill both young and adult prairie dogs (Hillman 1968). Progulske (1969) observed a prairie dog bite an adult male BFF on the face. The facial cuts on BFFs we saw could have been inflicted similarly.

Social Behavior

Social behavior refers to the interaction of two or more conspecifics. Interaction means that the animals are mutually influencing one another through some form of communication system (Eisenberg 1968).

Reproductive behavior.—We did not observe this, but snow tracking suggested that breeding activity began in mid-February and continued through March (as calculated from

the timing of litter emergence, estimated preemergence occupancy (45 days), and known gestation of 42-45 days (Hillman and Carpenter 1983). The initiation of reproductive activity in spring is further supported by the fact that an adult male BFF road-killed in early March near our main study area showed testicular mitotic activity but no spermatozoa, indicating that spermatogensis was just beginning (Thorne 1982, personal communication). Also in February and March, we noted BFF movements tended to increase as did activity area sizes and marking (Richardson et al., unpublished data) (Appendix). In South Dakota the exact timing of mating was unknown (Henderson et al. 1969), but captive BFFs bred in March and early April (Hillman and Carpenter 1983). Breeding behavior in captivity is described by Hillman and Carpenter (in Hillman and Clark 1980).

Ontogeny of young and maternal behavior.—The duration of time that young BFFs remain in the natal burrow before emerging above ground is unknown but is estimated at about 45 days. On 28 June 1982 a female moved a three-kit litter about 20 m from one hole to another. She carried one kit at a time in her mouth in three trips totaling 15 mins. The young were quite small (est. 200 g). In mid-July young in 11 litters appeared half- to three-fourths grown (est. 400–500 g). Nothing is known of BFF development between birth and first appearance above ground.

Mother BFFs may interact in a variety of ways with their young. In July, shortly after young began appearing above ground, mother BFFs commonly pulled young BFFs out of a burrow with her teeth and dragged them by their napes to other holes. On 11 July 1984 we watched a female with four halfgrown young at a burrow. Generally the young crawled on their bellies (eves barely reflecting our spotlight) in an area around the female while she remained standing alert watching our spotlight. At times they would all go down a nearby prairie dog hole, but reappeared three times. One time, she stood on all four feet exceptionally still while the young crawled all over her especially at her belly (nursing?) and this lasted about three minutes. Until late July, while probably still nursing, females "coaxed" up to four young out of a burrow and led them single file in "train behavior" (also noted by Henderson et al. 1969) across the prairie to a new site. On four occasions in July females brought dead prairie dogs to their young. On several occasions when a litter was above ground, the mother vocalized, after which all young rapidly descended into the burrow. When young are older, from late July to early August, litter mates are often seen separated—either in separate holes or one traveling with the female. On our approach she typically brought the group together by retrieving a lone juvenile or bringing the juveniles with her to the other juveniles and then keeping them all down, while she watched us.

Play.—Young BFFs in play were very quick with a variety of flexible, elastic body movements (Fig. 1). They played at night and in daylight. Play was the most often observed social behavior and was common in late July and early August. We categorized the types of play (1) object play, (2) autoplay, and (3) social play (even though the first two types are nonsocial, they are included here for completeness of play descriptions). In object play young BFFs exhibited close orientation and visual, oral, or olfactory inspection or manipulation of physical objects. One young BFF repeatedly "attacked" marker flags by jumping at them, front legs extended and mouth open.

In autoplay young BFFs moved forward and backward, with legs sometimes down together, back arched, chasing their own tails while turning their bodies around and around, rolling over on the ground, and changing position by "snapping" their bodies into the air at split-second intervals.

In social play two or more young BFFs engaged in approach-withdrawal (noncontact) or rough-and-tumble (contact) play, with the recipient of the play initiation either avoided or joined (Fig. 1). In approach-withdrawal play they constantly alternated distance between themselves as they chased and bounded forward and backward. The role of the pursuer and pursued were frequently interchanged within a single session. In these encounters mouths were sometimes open, the head was held from above to below the height of the shoulders, the tail was often extended with hairs erect, and the back was arched high (Fig. 1). No vocalizations were heard, possibly be-

cause we were too distant to hear them. This form of play occasionally followed or preceded rough-and-tumble play, in which young BFFs bit and tumbled with their interlocked bodies rolling about. Play activity occurred on and off burrow mounds and lasted up to 20 mins.

Young BFFs also exhibited a "stiff-legged dance" form of play in which they alternated approach-withdrawal among themselves and once toward a human. The limbs were alternately stamped against the ground, first one or both front feet and then one or both hind feet.

Hillman (1968) noted that young BFFs played above ground, running in and out of burrows in pursuit of one another. They bit and pulled at each other, humped their backs, and ran on their toes, often turning in circles, attempting to bite their tails. Henderson et al. (1969) noted one young BFF executed a midair somersault similar to what we observed.

Scent-marking.—Scent-marks have been observed in the snow (Richardson et al., unpublished data), but marking behavior is rarely observed (Appendix). One adult male was observed marking near a burrow opening in July 1984. On a grass substrate, he dropped his pelvic region on the ground with his tail extended straight behind him, the tip about 12 cm off the ground. He moved forward about 20 cm, mainly using his forelegs while dragging and wiggling his pelvic region against the substrate. He then scraped backward with his hind feet about four times over this area. This behavior was repeated twice more in two different grassy areas. After that, he moved to a small bush over which he extended his whole body, such that the neck, abdomen, and pelvis were rubbing into and wiggling through the bush. After a vigorous rubbing, he moved his forelegs and abdomen off the bush, leaving his pelvic region on the bush and rubbing into it another 3 sec. He circled around and repeated this marking behavior on the same bush two more times. The BFF may also have urinated on the bush during the rubbing procedure. Each marked area exuded a strong musk odor. This behavior may have been in response to the observer standing 5 m away. After the marking behavior, the BFF moved away slowly to explore new burrows.

Agonistic Behavior.—Agonistic behavior (conflict between two animals; Scott 1962) was not observed by us or the South Dakota researchers.

Human-Ferret Interactions

Ferret responses to human activities varied. When spotlighted BFFs generally oriented toward the light and vehicle, at least momentarily. Some moved to or stayed in prairie dog burrows, some retreated into burrows for extended periods, and some continued their activities. When BFF heads were visible out of a hole, their eyes were often turned away from the light, perhaps avoiding the direct beam. Family groups were shy in mid-July but tended to be less shy later. Juveniles seemed to be more shy in our presence than adults. One BFF spotlighted at 75 m appeared to direct an "agoniso the observer standing 5 m way. After the marking behavior, the BFF lowly to explore new burrows.

ea. This behavior was repeated twice more in different grassy areas. After that, he moved to approached to within 2 m of us in our vehicle and on one occasion walked under the truck.

When approached on foot, BFF responses again varied. During daylight they typically retreated to burrows, observed us for short periods from the hole, and then descended the burrow. However, the distance from us at which BFFs retreat to burrows varied from 10 to 100 m. Again, juveniles appeared more shy. During daylight young BFFs popped their heads out of burrows, apparently observing passers-by within 100 m, but retreated if the observer approached directly. One adult female was followed at 10 m on hunting forays on 14 occasions with no apparent alteration in her behavior because of our presence. At night several individuals, both juveniles and adults, were quietly and slowly approached in the spotlight beam or with flashlights to within 5 m. BFFs were wary of us, stayed near holes, and "hissed" at us but overall seemed curious about our activities. Whereas some BFFs later retreated to burrows, others moved slowly between burrows. BFF response to spotlighting disturbances was briefly evaluated by Campbell et al. (1985).

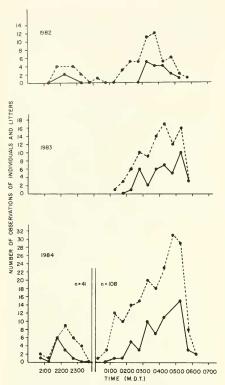


Fig. 3. Observation frequencies (by 0.5 hr intervals) for ferret litters (solid line) and single individuals and litters (dash line) on full night surveys (1982), partial night surveys (1983) (observer nights = 41), and late night surveys (1984) (observer nights = 108).

Vocalizations

BFFs emit several sounds heard by us and reported in previous studies. Based on the source and the context, we classified calls as: (1) threat, (2) defense, (3) greeting, (4) mating, and (5) sounds by young. We heard calls we labeled "bark," "huff-hiss," "growls," "ungh," and "chattering-bark." Hillman (1968) heard a "hiss," "snarl," and "bark." Henderson et al. (1969) heard an "ungh" (adult ferret to her young) and a "noise" (among young playing in a burrow). Progulske (1969) heard a "chatter" and a "low hiss." Finally, Hillman and Carpenter (1983) noted a "whimpering" (in copulation). Because contextual definitions are in-

complete for each call, we did not assign each call to a "functional" category.

Activity Patterns

Activity was defined as any appearance of BFFs above ground. The way in which a population structures its activity patterns reflects its survival strategy (Orians 1961). We readily located BFFs during most months, including winter, but, like others (Hillman 1968, Henderson et al. 1969, Fortenbery 1972), we found that the animals themselves are easiest to locate during summer. Hillman (1968) found BFFs most active in late evening (1900–2400) and early morning (0200–0600). Frequency of BFF observation from spotlight searches conducted during July-August from 1982–1984 are shown in Figure 3.

Snowtrack evidence and direct observation showed that BFFs were active after sunrise in winter. In July BFFs were observed to be active until 1200. We watched one BFF and her litter of four for 14 consecutive mornings. She became active each morning around 0830, 2 hr after sunrise, and hunted for an hr or more. After 0930 in July, BFFs made surface appearances for short durations off and on until 1200 and rarely in the afternoon. Also, the same BFFs were often visible at the same hrs and in the same locations.

BFFs were active above ground in temperatures of -38 C, during snow and rainstorms, and in winds up to 50 kph. Richardson et al. (unpublished data) concluded that temperature did affect BFF movements. Activity patterns of radio-tagged BFFs were described by Biggins et al. (1985).

DISCUSSION

Although the Wyoming BFF population and the one formerly in South Dakota are associated with different prairie dog species, live in different biogeographic areas, and are under different climatic regimes, much of their gross behavior and activity patterns are similar. Even though a systematic description of BFF behavior was not previously available, our categories allow for inclusion of BFF observations from South Dakota. The BFF is difficult to observe, generally being nocturnal and appearing above ground at irregular intervals and for irregular durations. Thus, our

ethogram and activity data are incomplete, but BFF behavior apparently is similar to related species and much BFF behavior is probably homologous to other species of Mustela. Where behavioral data are currently lacking for BFFs (e.g., reproductive, agonistic, and ontogenetic behaviors), the most complete literature on related mustelids can be used to suggest BFF behavior patterns until observational data for the rare BFF become available. Furthermore, a comparative behavioral approach, as discussed by Eibl-Eibesfeldt (1970) and previously elucidated by Remane (1952), allows identification of homologous behavior patterns if they occur in a large number of closely related species.

Steppe ferrets live in large ground squirrel (suslik; *Spermophilus* spp.) colonies, similar to prairie dog colonies, but, in contrast to BFFs, distinctive deposition of excavated subsoil by steppe ferrets is not mentioned in the literature even though steppe ferrets do dig out susliks in winter (Stroganov 1969).

Feces and urine are deposited by BFFs as waste products but may also serve in "scent marking" (Macdonald 1980). Currently it is impossible to distinguish between feces and urine as elimination products or scent marks (see Wells and Bekoff 1981).

Steppe ferrets and BFFs hunt similarly (this study, Hillman 1968, Henderson et al. 1969). Killing methods of *M. frenata*, *M. erminea*, *M. rixosa*, *M. vison*, and *M. putorius* are basically similar (Iwen 1958). Predatory behavior of *M. nivalis*, *M. erminea*, and *M. putorius* is similar, especially for the two weasels (Gossow 1970). The killing procedure for *M. nivalis* is generally very rapid, ranging from 10 to 60 sec (Heidt 1970). Ewer (1973) characterized all mustelids as solitary, opportunistic predators whose hunting behaviors include a "random search" foraging pattern and a neck bite for killing.

The lack of "aggressive" behavior by the male BFF during copulation was unlike that for *M. eversmanni* and *M. putorius* (Hillman and Carpenter 1983). Other mustelid species display a copulatory pattern similar to that described for BFFs (e.g., Wright 1948, for *M. frenata*; Hartman 1964, for *M. nivalis*; and Rowe-Rowe 1977, for *Ictonyx striatus* and *Poecilogale albinucha*). The timing of BFF reproductive activity, as suggested by our ob-

servations, corresponds well with observations of Henderson et al. (1969) and Hillman and Carpenter (1983) for the BFF and is similar to the seasonality of reproductive activity for *M. putorius* (Walton 1976, Danilov and Rusakov 1969).

BFF growth curves, unknown at present, may be estimated based on limited data for the steppe ferret (Sviridenko 1935), our limited observations, data from the South Dakota ferret studies (Henderson et al. 1969), and from other mustelid studies (e.g., East and Lockie 1964, 1965).

Young of several mustelid species perform certain behaviors in play that probably serve them in predatory and other behaviors as adults (Gassow 1970). Play by P. albinucha and I. striatus was mainly aggressive, involving actions typical of adult fighting, prey capture, and killing (Rowe-Rowe 1977). The aggressive play of M. putorius appears similar to our observations and those of BFF in South Dakota. Mustela putorius young exhibited all three types of play (Poole 1970) that we described for M. nigripes. BFF play probably contains many of the motor components exhibited by adults in agonistic and reproductive behaviors, but because of the secretive, solitary, nocturnal habits of free-living BFFs, these motor patterns in an adult context are virtually impossible to observe.

The stiff-legged dance we described for young BFFs corresponds to similar behavior in *M. nivalis* (Heidt 1970) and in *Martes* spp. (Schmidt 1943), in which cases the behavior pattern was thought to be agonistic. Agonistic behavior has been extensively studied in *M. erminea* (Erlinge 1977), *M. putorius*, and *M. furo* (Poole 1966, 1967, 1972a,b, 1973, 1974) and provides descriptions that may be similar to BFFs. Our listing of vocalizations for BFFs and those from South Dakota are generally comparable to vocalizations for other mustelids (Gossow 1970, Huff and Price 1968, Svendsen 1976, Goethe 1974, Channing and Rowe-Rowe 1977, Belan et al. 1978).

Daily and seasonal activity for the Wyoming BFFs varied somewhat from that for South Dakota BFFs. Time allocation by a species reflects differences in habitat and social organization (e.g., Greenlaw 1969, Post and Baulu 1978). Our data on tracks, scats, and activity patterns have implications for conducting

BFF surveys, which are discussed elsewhere (Clark et al. *Handbook of methods*, 1984). We sought to minimize our direct contact with BFFs to reduce research impacts. Even though our data adds to an understanding of BFFs, much yet remains to be learned, including more complete behavioral descriptions and quantification of our ethogram. But, as noted by Marler (1968), the building up of descriptions is itself a quantitative process and an essential first step in revealing the behavior and ecology of a species.

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Appendix

Photographs of black-footed ferrets illustrating various behaviors and ferret signs.



A. Adult female ferret and young male in alert (by Tim Clark).



B. Ferret walking (by Doug Brown).



C. Adult female in alert (by Tim Clark).



D. Adult female with prairie dog she just killed (by Tim Clark).



E. Adult female in alert (note tick in ear) (by Tim Clark).



F. Adult female emerging from burrow with just-killed prairie dog (by Tim Clark).



G. Adult female with prey—prairie dog (by Tim Clark).



H. Adult female with prey—prairie dog (not a throat bite) (by Tim Clark).



I. Juvenile ferret alert in prairie dog hole (by Tim Clark).



J. Adult ferret hunting prairie dogs (by Tim Clark).



K. Ferret dragging dead prairie dog back to her natal burrow containing some of her young (by Tim Clark).



L. Alert ferret (by Tim Clark).



M. Ferret snow marking. Tracks in photo indicate a ferret scraped or scratched through the snow into the substrate in a circular area (foreground about 25 cm diameter), made a trough in the snow with its body, and rubbed its body over and through the small shrub in background. Considered a scent-marking behavior (by Tim Clark).



N. Ferret snow marking and dirt scrape. Tracks indicate that a ferret entered the prairie dog burrow (hole diameter 10 cm), excavated a small amount of subsoil onto the snow (dirt scrape), and moved 0.3 m away from the burrow where it scraped or scratched through the snow within a roughly circular area, probably a scent-marking behavior. Note ferret tracks exiting upper left (by Louise Richardson).



0. A type of ferret digging. A ferret excavated subsoil from within a prairie dog burrow. Ferrets pull dirt out of the burrow holding it against their chests with their forepaws as they move backward, depositing the dirt in a linear fashion away from the burrow opening and sometimes making a distinctive trough or "trench" within the excavated subsoil. Digging length is about 1.5 m (by Tim Clark).



P. A ferret rubbed its body over and through the shrub in foreground (shrub about 22 cm high and 30 cm wide), with ferret tracks evident around the base of the shrub. Behind the shrub and to the right is a patch where the ferret scraped or scratched through the snow into the substrate (snow marking about 20 cm in diameter). Both markings are probably scent marking (by Louise Richardson).



Q. A ferret kill drag. Ferret entered burrow (dark area in foreground about 50 cm in diameter) from right (note dual print tracks), apparently killed a prairie dog in the burrow, and dragged it out and away from the burrow with tracks exiting to the left. The trough like depression (about 18 cm wide) was from the prairie dog's body being drug in the snow by the ferret, whose tracks are seen along the left side of the slide marks (by Tim Clark).

LITERATURE CITED

- ALCOCK, J. 1975. Animal behavior: An evolutionary approach. Sinauer Assoc., Inc. Sunderland, Mass. 547 pp.
- BALPH, D. F., AND A. W. STOKES. 1963. On the ethology of a population of Uinta ground squirrels. Amer. Midl. Nat. 69:106–126.
- BELAN, I., P. N. LEHNER, AND T. W. CLARK. 1978. Vocalizations of the American pine marten, Martes americana, J. Mammal. 59:871–874.
- BIGGINS, D., M. H. SCHROEDER, S. C. FORREST, AND L. RICHARDSON. 1985. Movements of radio-tagged black-footed ferrets. Pages 11.1–11.17 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.
- CAMPBELL, T. M. III. D. BIGGINS, S. C. FORREST, AND T. W. CLARK. 1985. Spotlighting as a method to locate and study black-footed ferrets. Pages 24. 1–24.7 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.
- Candland, D. K. 1974. The physiological ethogram. Bull. Psychonomic Soc. 18:264–265.
- Channing, A., and D. T. Rowe-Rowe. 1977. Vocalizations of South African mustelines. Z. Tierpsychol. 44:283–293.
- CLARK, T. W., T. M. CAMPBELL, M. H. SCHROEDER, AND L. RICHARDSON. 1984. Handbook of methods for locating black-footed ferrets. Wyoming BLM Tech. Bull., Cheyenne, No. 1, 55 pp.
- CLARK, T. W., L. RICHARDSON, D. CASEY, T. M. CAMPBELL, AND S. C. FORREST. 1984. Seasonality of blackfooted ferret diggings and prairie dog burrow plugging. J. Wildl. Manage. 48: 1441–1444.
- DANILOV, P. I., AND O. S. RUSAKOV. 1969. Special aspects of the ecology of the polecat (*Mustela putorius*) in the northwestern region of the European USSR. Zool. Zh. 48:1383–1394.
- EAST, K., AND J. D. LOCKIE. 1964. Observations on a family of weasels (M. nivalis) bred in captivity. Proc. Zool. Soc., London. 143:359–363.
- . 1965. Further observations on weasels (*M. nivalis*) and stoats (*M. erminea*) born in captivity. Proc. Zool. Soc., London. 147:234–238.
- EIBL-EIBESFELDT, I. 1970. Ethology: the biology of behavior. Rinehart & Winston, New York. 530 pp.
- EISENBERG, J. F. 1968. Behavior patterns. Pages 451–495 in J. A. King, ed., Biology of *Peromyscus* (Rodentia). Amer. Soc. Mammal. Spec. Publ. No. 2.
- ERICKSON, R. C. 1973. Some black-footed ferret research needs. Pages 153–164 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.
- ERLINGE, S. 1977. Agonistic behavior and dominance in stoats (*Mustela erminea L.*). Z. Tierpsychol. 44: 375–388.
- EWER, R. F. 1973. The carnivores. Weidenfeld and Nicholson, London. 494 pp.

- FORTENBERY, D. K. 1972. Characteristics of the blackfooted ferret. USDI Res. Publ. No. 109, 8 pp.
- GOETHE, F. 1964. Das verhalten dei musteliden Handb. Zool. Berl. 8:1-80.
- Gossow, H. 1970. Vergleichend verhaltensstudien und marderartigen 1. über lautausserungen und zum beuteverhalten. Z. Tierpsychol. 27:405–480.
- GREENLAW, J. S. 1969. The importance of food in the breeding systems of the rufous-sided towhee, Pipilo erythrophtalmus (L.). Unpublished dissertation, Rutgers University, 169 pp.
- HARTMAN, L. 1964. The behavior and breeding of captive weasels (*Mustela nivalis* L.). New Zealand J. Sci. 7:147–156.
- HEIDT, G. A. 1970. The least weasel Mustela nivalis Linnaeus: development biology in comparison with other North American Mustelida. Michigan State University Publ. Biol. Sci. 4:229–282.
- HENDERSON, F. R., P. F. SPRINGER, AND R. ADRIAN. 1969. The black-footed ferret in South Dakota. South Dakota Dept. Game, Fish, and Parks, Pierre. 37 pp.
- HILLMAN, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Trans. N. Amer. Wildl. and Nat. Res. Conf. 33:346–349.
- HILLMAN, C. N., AND R. L. LINDER. 1973. The black-footed ferret. Pages 10–23 in R. L. Linder and C. N. Hillman, eds., Proc. Black-footed Ferret and Prairie Dog Workshop, South Dakota State University, Brookings.
- HILLMAN, C. N., AND J. W. CARPENTER. 1983. Breeding biology and behavior of captive black-footed ferrets, Mustela nigripes. Int. Zoo Yrbk. 23:186–191.
- HILLMAN C. N. AND T. W. CLARK. 1980. Mustela nigripes. Mammal. Species No. 126. 4 pp.
- HUFF, J. N., AND E. O PRICE. 1968. Vocalizations of the least weasel, Mustela nivalis. J. Mammal. 49:548–550.
- IWEN, F. 1958. Killing methods of mustelids. Unpublished thesis, University of Wisconsin, Madison. 39 pp.
- KLOPPER, P. H., AND J. P. HAILMAN. 1967. An introduction to animal behavior. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 297 pp.
- LEHNER, P. N. 1979. Handbook of ethological methods. Garland Press, New York, New York. 403 pp.
- MacDonald, D. W. 1980. Patterns of scent marking with urine and facces amongst carnivore communities. Symp. Zool. Soc., London, 45:107–139.
- MARLER, P. 1968. Observation and description of behavior. In E. O. Price and A. W. Stokes, eds., Animal behavior in laboratory and field. W. H. Freeman and Co., San Francisco, California, 130 pp.
- Orians, G. 11 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Mongr. 31(3):285–312.
- Poole, T. B. 1966. Aggressive play in polecats. Symp. Zool. Soc., London 18:23-44.
- _____. 1967. Aspects of aggressive behavior in polecats. Z. Tierpsychol. 24:351–369.
- Z. Tierpsychol. 24:351–369.

 ——. 1970. Polecats. HMSO, London, Forestry Comm.
 Forest Record 76:1–17.
- 1972a. Some behavioral differences between the European polecat, Mustela putorius, the ferret M. furo, and their hybrids. J. Zool., London 166: 25, 35.

- _____. 1972b. Diadic interactions between pairs of male polecats (Mustela furo and M. furo X M. putorius hybrids) under standarided environmental conditions during the breeding season. Z. Tierpsychol. 30:45–58.
- 1973. The aggressive behavior of individual male polecats (Mustela putorius, M. furo, and hybrids) towards familiar and unfamiliar opponents. J. Zool., London 170:395—414.
- 1974. Detailed analysis of fighting in polecats (Mustelidae) using cine film. J. Zool., London 173:369–393.
- Post, W., and J. Baulu. 1978. Time budgets of Macaca mulatta. Primates 19:125–140.
- Progulske, D. R. 1969. Observations of a penned, wildcaptured black-footed ferret. J. Mammal. 50: 619–620.
- REMANE, A 1952. Der Grundlagen das naturlichen Systems der vergleichenden anatomie und phylogenetik. Leipzig. 364 pp.
- RICHARDSON, L., T.-W. CLARK, S. C. FORREST, AND T. M. CAMPBELL III. 1985. Snowtracking as a method to search for and study the black-footed ferret. Pages 25.1–25.11 in S. Anderson and D. Inkley, eds., Black-footed Ferret Workshop Proc., Laramie, Wyoming, September 18–19, 1984. Wyoming Game and Fish Publ., Cheyenne.
- ROWE-ROWE, D. T. 1977. Reproduction and post-natal development of South African Mustelines (Carnivora: Mustelidae). Zoologica Africana 13: 103–114.

- SCHMIDT, F. 1943. Natural history of the spruce and stone martens: with comparative observations on their nearest relatives, especially the Siberian sable and the American pine marten. Publ. Inst. fur Jagdkunde der Univ., Gottingen. 268 pp.
- SCOTT, J. P. 1956. The analysis of social organization in animals. Ecology 37:213–221.
 - 1962. Introduction to animal behavior. In E. S. E. Hafez, ed., The behavior of domestic animals. Williams and Wilkins Co. Baltimore, Maryland. 619 pp.
- SHEETS, R. G., AND R. L. LINDER 1969. Food habits of the black-footed ferret (*Mustela nigripes* in South Dakota. Proc. South Dakota Acad. Sci. 48:58–61.
- STROGANOV, S. U. 1969. Carnivorous mammals of Siberia. Acad. Sci. USST, Siberia Branch, Biol. Inst. 381–394.
- SUSTARE. D. 1975. Classification of behavioral units. Paper presented in Symposium on Quantitative methods in ethology. Anim. Behav. Soc. Meeting 23 May 1975, Wilmington, North Carolina.
- SVENDSEN, G. E. 1976. Vocalizations of the long-tailed weasel (Mustela frenata). J. Mammal. 57: 398–399.
- SVIRIDENKO, P. 1935. The light ferret (*Putorius evers-manni*) and its economic importance. USSR Publ.
- WALTON, K. C. 1976. The reproductive cycle in the male polecat *Putorius putorius*. J. Zool. London 180: 498–503.
- Wells, M. C., and M. Bekoff. 1981. An observational study of scent-marking in coyotes *Canis latrans*. Anim. Behav. 29:332–350.
- WRIGHT, P. L. 1948. Breeding habits of captive long-tailed weasels (Mustela frenata). Amer. Midl. Nat. 39: 338–344.